

FIELD STUDIES ON DIURNAL LEAF DIFFUSIVE RESISTANCE OF MANGROVE LEAVES AT VARIOUS SOIL MOISTURE TENSIONS AND PHOTOSYNTHETICALLY ACTIVE RADIATION

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ABSTRACT

Diurnal trends in leaf diffusive resistance of two mangrove species, *Avicennia marina* (Forsk.) Vierh. and *Bruguiera gymnorhiza* (L.) Lam., were investigated at varying moisture levels and photosynthetically active radiation (PAR). Generally, diffusive resistance decreased from early morning till midday as PAR increased. After midday, resistance increased primarily as a result of decreasing PAR and increasing soil moisture tensions. Tidal inundation of the mangroves did not have any measureable effect on diffusive resistance at low PAR and at low soil moisture tensions. Under conditions of high PAR and high soil moisture tensions tidal coverage of the swamp relieved soil moisture stress and resulted in decreased leaf diffusive resistance.

UITTREKSEL

VELDSTUDIES VAN DAAGLIKSE BLAARDIFFUSIEWEERSTAND VAN MANGLIETBLARE BY VERSKILLEND VOGSPANNINGS EN FOTOSINTETIESE-AKTIWE STRALING

Daaglikse verloop van blaardiffusieweerstand van twee manglietsoorte. *Avicennia marina* (Forsk.) Vierh. en *Bruguiera gymnorhiza* (L.) Lam. is by wisselende voggehaltes en fotosintetiese-aktiewe straling (FAS) ondersoek. Oor die algemeen het diffusieweerstand afgeneem vanaf vroeg oggend tot middag, soos FAS toegeneem het. Na die middag-uur het weerstand toegeneem, primêr as gevolg van vermindering in FAS en toenemende grondvogspannings. Getyoorstrominge van die mangliete het geen meetbare uitwerking op diffusieweerstand by lae FAS en lae grondvogspannings gehad nie. Onder omstandighede van hoë FAS en hoë vogspannings het getybedekking van die moeras die grondvognoed verlig en verminderde blaardiffusieweerstand tot gevolg gehad.

INTRODUCTION

Mangroves in intertidal zones are regularly inundated by sea water which has a high osmotic potential. Yet, very little information is available on the stomatal responses of these plants to marked diurnal fluctuation in substrate moisture levels and osmotic potentials. Apparent transpirational rhythms in the white mangrove, *Avicennia marina* were investigated using simple potometric methods (Lewis & Naidoo, 1970; Steinke, 1979). The disadvantage of the potometric method is that it does not provide an absolute figure for the loss of water by the plant. In addition, a potometer records water absorption by a transpiring

branch. Conclusions drawn from water absorption data from the base of a transpiring branch cannot be directly applied to stomatal responses unless data are recorded at the leaf surface.

Studies on water relations in mangroves have been concerned mainly with the effects of salinity. Scholander *et al.* (1965) and Scholander (1968) determined osmotic potentials and xylem potentials in some mangrove species. Miller (1974) reported that stomata of mangrove species in Florida respond differently to different salinities.

The aim of this investigation was to determine the diurnal adjustments in stomatal responses of two local mangrove species, *Avicennia marina* and *Bruguiera gymnorhiza*, to varying soil moisture levels and photosynthetically active radiation.

MATERIAL AND METHODS

Field measurements were carried out during April and May of 1979 at the Beachwood mangrove area, Durban. Mangrove trees 3.5 to 4.5 m tall were selected for data collection. To investigate the effects of varying soil moisture tensions on stomatal responses, measurements were made on trees growing in soils that were continuously moist and regularly inundated, and on trees that were growing in relatively dry areas inundated only during high spring tides. The leaves selected for measurements were located at the tips of branches that were approximately 1.5 m above ground level. All measurements were made hourly.

Leaf diffusive resistances were measured with a diffusion porometer (Lambda Instruments Inc., Model No. Li 65, Lincoln, Nebraska) with a horizontal sensor cup. The porometer was calibrated by prescribed procedures both before and after measurements were taken. To ensure that porometer data were reliable, procedures and precautions described by Kanemasu *et al.* (1969) and Morrow & Slatyer (1971) were followed. Since both *Avicennia* and *Bruguiera* are hypostomatous, diffusive resistance was determined for the abaxial surface only. Adaxial resistance for both mangrove species was usually greater than 50 s cm^{-1} . The stomatal frequency for both species was about 180 stomata mm^{-2} .

During each porometer reading measurements were made of the light incident on the adaxial surface of the leaf with a quantum light meter (Lambda Instruments Inc., Model No. Li 185, Lincoln, Nebraska). The quantum sensor measures photosynthetically active radiation (PAR) in units of microEinsteins per square metre per second ($\mu\text{E m}^{-2} \text{ s}^{-1}$).

Soil moisture tension was determined by Gallenkamp soil tensiometers which were buried in the ground to a depth of 200 mm at the base of trees which were being sampled. The tensiometers were prepared by following procedures recommended by the manufacturers. Usually, tensiometers were left overnight for equilibration.

Stomatal imprints were obtained with cellulose acetate diluted with amyl acetate. The imprints were removed with transparent sticky tape, placed on stubs, coated with gold and examined with a scanning electron microscope.

All measurements were made on clear sunny days. Wind speed, relative humidity, temperature, tidal levels and salinity of the tidal water were also noted. Temperatures during data collection varied between 25° to 30°C.

RESULTS AND DISCUSSION

In most cases results were similar for *Avicennia* and *Bruguiera*; therefore the results presented for one are representative of the other.

Data in Figure 1 represent typical responses of *Avicennia* on a day on which

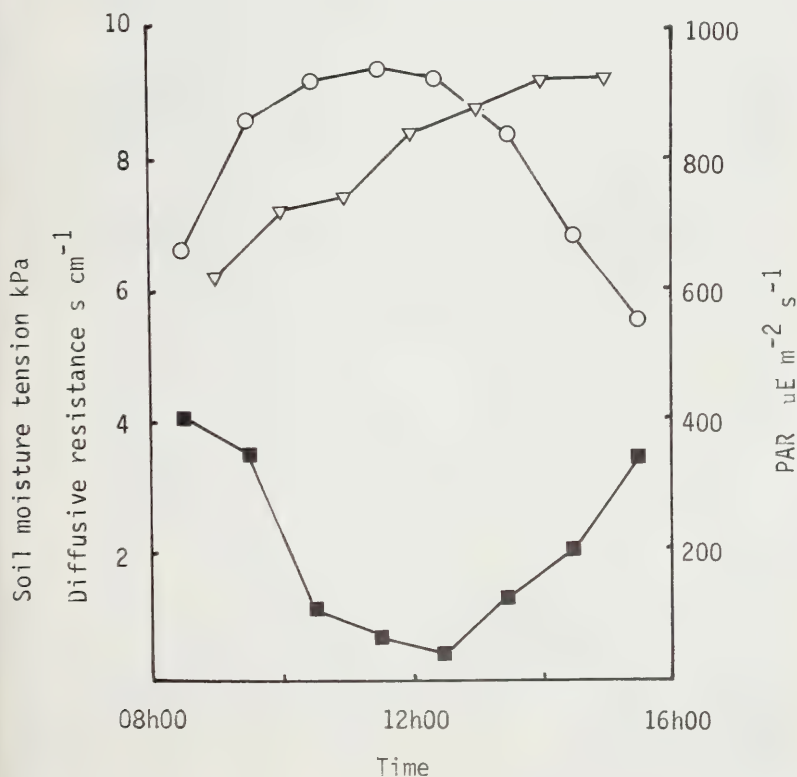


FIG. 1.

Diurnal trends in diffusive resistance (■—■), PAR (○—○) and soil moisture tension (▽—▽) of *A. marina* on 10/4/79. No tidal coverage.

no tidal inundation occurred. Leaf diffusive resistance decreased from 08h00 to 12h00 in response to increasing PAR. During the sampling period the soil moisture content was below field capacity (>6 kPa). Thereafter, leaf diffusive resistance increased as a result of decreasing PAR and increasing soil moisture tension. Plants had probably reached a state of incipient wilting at high soil moisture tensions resulting in stomatal closure.

Similar results were obtained for *Bruguiera*. Hourly observations of stomatal imprints (Fig. 2 A & B) for *Bruguiera* confirmed that stomata were maximally open at midday. At maximal stomatal opening the width of the aperture was $11\mu\text{m}$.

Unfortunately, it was not possible to make stomatal imprints of the abaxial surface of *Avicennia* leaves because of the numerous pedicellate hairs present on the surface (Fig. 2 C & D). Others (Lewis & Naidoo, 1970; Steinke, 1979) reported that *Avicennia* exhibits a mid-morning maximum. However, these workers used potometric techniques which measured apparent transpiration and not direct loss of water from the leaf surface. Diffusion porometers on the other hand characterize responses of stomata with direct reference to the transpiration process (Van Bavel *et al.*, 1965).

Trends in diffusive resistance for *Avicennia* under very low soil moisture tensions and low PAR are shown in Figure 3. Diffusive resistance decreased with increase in PAR, as in Figure 1, reaching minimum resistance at noon. Subsequent rapid decrease in PAR caused a rapid increase in diffusive resistance. Tidal coverage of the swamp during the early afternoon had no effect on diffusive resistance probably because of the low soil moisture tension. That the soils were waterlogged during the whole morning is indicated by soil moisture tension values of less than 4 kPa. Similar results were obtained for several *Avicennia* and *Bruguiera* trees under similar conditions of PAR and soil moisture tension.

In Figures 4 and 5 stomatal responses followed the usual pattern, the resistance decreasing till midday as PAR increased. After midday the leaf resistance began to increase primarily as a result of decreasing PAR and increasing soil moisture tension. Tidal inundation of the swamp resulted in a second decrease in diffusive resistance for both *Bruguiera* (Fig. 4) and *Avicennia* (Fig. 5).

In *Bruguiera* the tidal effect on diffusive resistance occurred between 14h00 and 14h30. At this time the soil moisture tension was 10,6 kPa, which is well below field capacity, and the PAR value was $530\mu\text{Em}^{-2}\text{s}^{-1}$.

In *Avicennia* the tidal effect occurred after 13h00. At 13h00 the soil moisture tension was 8,7 kPa, which is again well below field capacity, and PAR was $780\mu\text{Em}^{-2}\text{s}^{-1}$. Decrease in diffusive resistance during tidal inundation thus occurred at high soil moisture tension and high PAR. The tidal effect on diffusive resistance was only observed on trees growing in relatively dry areas and well exposed to PAR. An incoming tide had no effect on diffusive resistance in Figure 3 because the soils were waterlogged and PAR was low ($375\mu\text{Em}^{-2}\text{s}^{-1}$).



FIG. 2.

Scanning electron micrographs of abaxial leaf surfaces.

- A. stomata of *B. gymnorrhiza* at 09h00
- B. stomata of *B. gymnorrhiza* at 12h00
- C. pedicellate hairs on leaf of *A. marina*
- D. a single pedicellate hair of *A. marina*

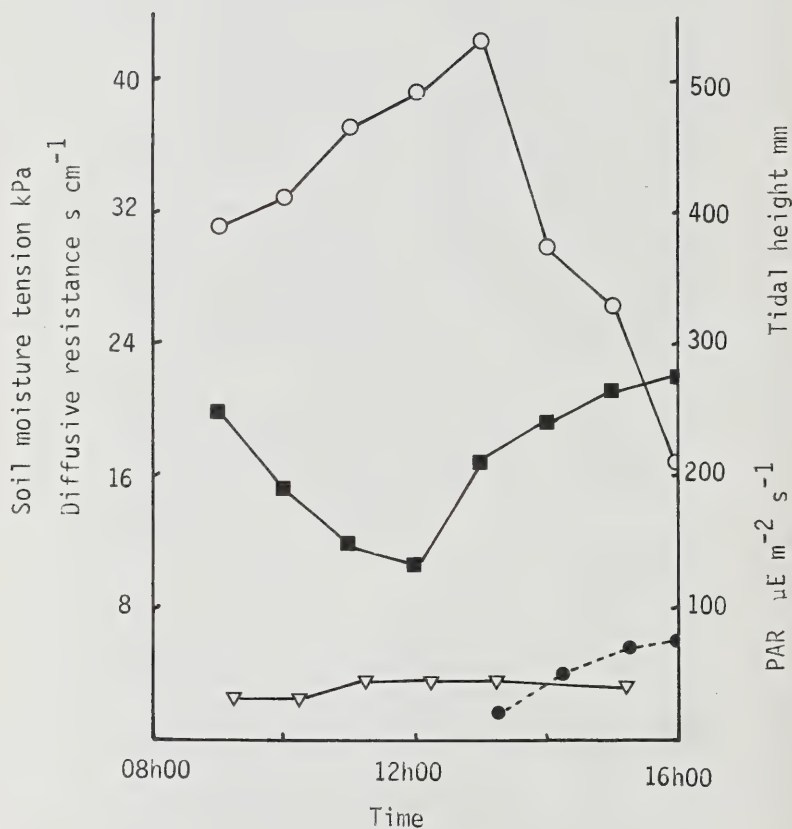


FIG. 3.
Diurnal trends in diffusive resistance (■—■), PAR (○—○) and soil moisture tension (▽—▽) of *A. marina* on 22/5/79. Tidal coverage (●—●).

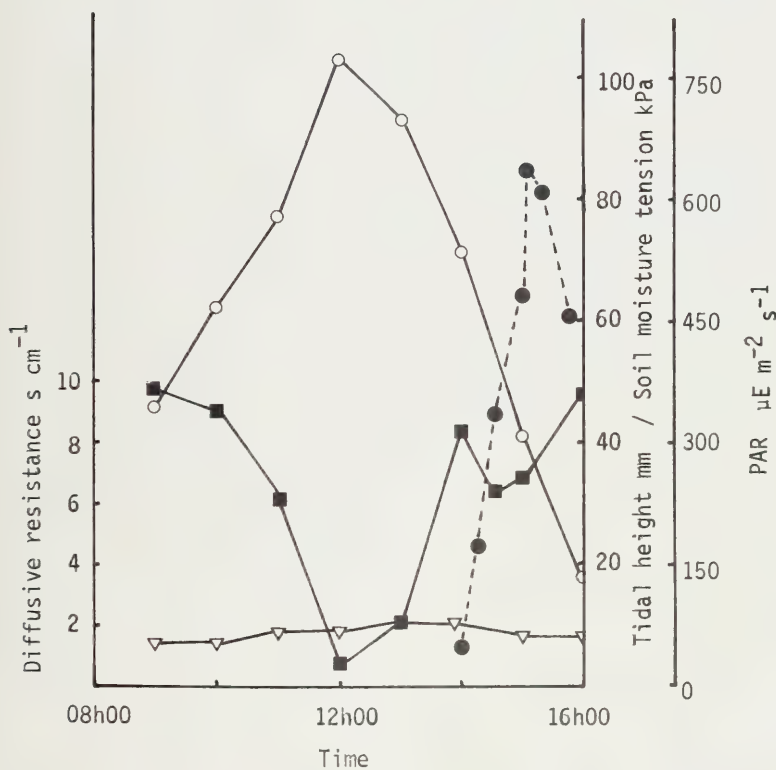


FIG. 4.

Diurnal trends in diffusive resistance (■—■), PAR (○—○) and soil moisture tension (▽—▽) of *B. gymnorrhiza* on 10/4/79. Tidal coverage (●—●).

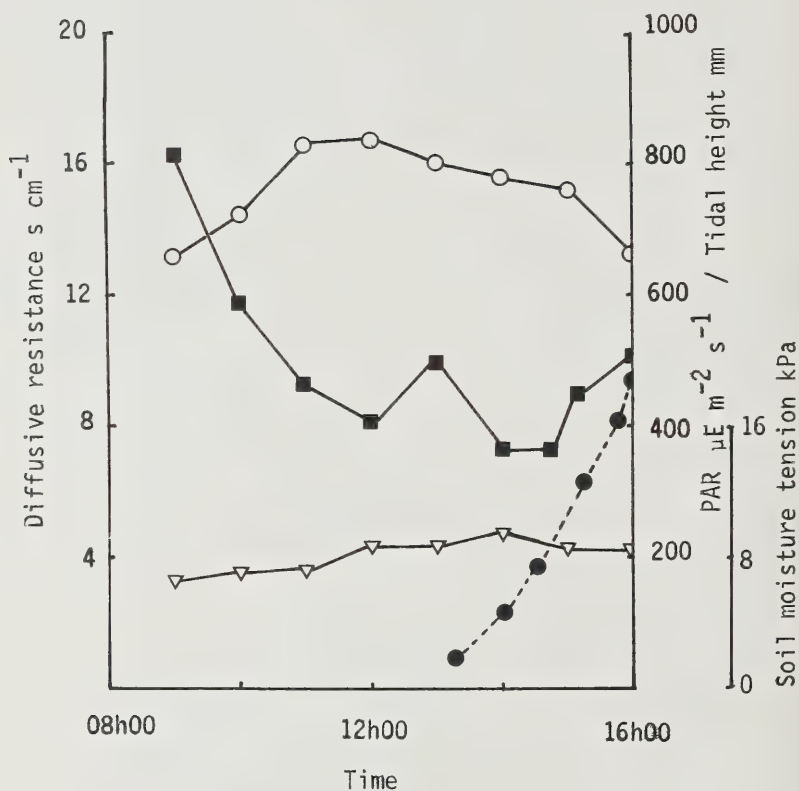


FIG. 5.
Diurnal trends in diffusive resistance (■—■), PAR (○—○) and soil moisture tension (▽—▽) of *A. marina* on 11/5/79. Tidal coverage (●-----●).

An increase in apparent transpiration rate in *A. marina* during tidal inundation was reported previously (Lewis & Naidoo, 1970).

The significant relationship between diffusive resistance and PAR for *Bru-guiera* under shaded and non-shaded conditions is shown in Figure 6. The regression line for shaded conditions shows that the resistance is greater at low PAR. For trees well exposed to PAR the diffusive resistance is considerably reduced. Thus there is a trend towards lower resistance at high PAR.

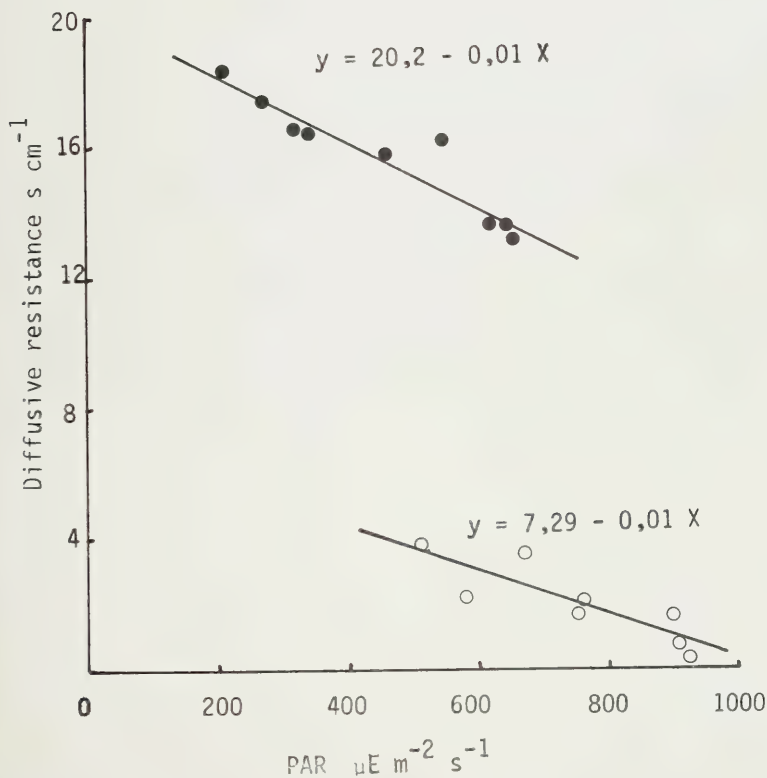


FIG. 6.

The relationship between leaf diffusive resistance and PAR for *B. gymnorhiza* under shaded (●) and non shaded (○) conditions. Each point is an average of three leaves.

Although mangroves inhabit a continuously moist environment their stomatal responses are similar to those of many other plants. In the field, stomatal responses are largely governed by irradiance and soil moisture stress (Meidner & Mansfield, 1968; Kanemasu & Tanner, 1969; Teare & Kanemasu, 1972; Denmead & Miller, 1976). These two factors largely determine the water potential gradient along the soil-plant-atmosphere continuum. Most plants would be under stress if swamped by sea water which has an osmotic potential of -2400 kPa. However, mangrove xylem sap has been shown to possess negative pressures of up to 6080 kPa (Scholander *et al.*, 1965). This supports our observation that tidal coverage of mangroves actually relieves soil moisture stress and subsequently results in decreased leaf diffusive resistance.

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